

Scotland's Rural College

The long-term development of temperate woodland creation sites: from tree saplings to mature woodlands

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The long-term development of temperate woodland creation sites: from tree saplings to mature woodlands

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3 ***The long-term development of temperate woodland creation sites: from tree saplings to***
4 ***mature woodlands***

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20 WrEN project.

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Abstract:

Tree planting is at the forefront of the current environmental agenda to mitigate climate change and tackle the biodiversity crisis. In the UK, tree planting has been a priority for more than a century and has helped increase woodland cover from a historic low of 5% at the beginning of the 20th century to a current figure of 13%. However, we still know relatively little about the long-term development of woodland creation sites (particularly of native woodlands) over ecologically realistic timescales. We surveyed a chronosequence of 133 temperate woodland patches encompassing 106 woodland creation sites (10–160 years old) and 27 mature ‘ancient’ woodlands (>250 years old), using a combination of field surveys and remote sensing techniques to quantify vegetation structural changes associated with woodland development. Woodland creation sites displayed similar vegetation development patterns to those described for other woodland systems, i.e. a gradual transition as woodlands undergo ‘stand initiation’, ‘stem exclusion’ and ‘understorey re-initiation’ stages, and became more similar to ‘ancient’ woodlands over time. Structural heterogeneity, average tree size and tree density were the attributes that varied the most among woodland developmental stages. In general, structural heterogeneity and average tree size increased with woodland age, whilst tree density decreased as would be expected. Younger sites in ‘stand initiation’ were strongly dominated by short vegetation, ‘stem exclusion’ sites by taller trees, and older sites had a more even vegetation height distribution. There was a large degree of overlap between the vegetation characteristics of woodlands in ‘understorey re-initiation’ stages and older ancient woodlands (partly driven by a lack of regeneration in the understorey); these results suggest that it takes between 80 to 160 years for woodland creation sites to develop certain vegetation attributes similar to those of mature ancient woodlands included in this study. Woodland management practices to create canopy gaps and reducing grazing/browsing pressure to promote natural regeneration are likely to accelerate this

46 transition, increase the structural heterogeneity and biodiversity value of woodland creation sites,
47 and enable adaptation and resilience to climate change.

For Review Only

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Introduction:

Long-term, large-scale deforestation has reduced global forest cover by 50% over the last three centuries (Ramankutty & Foley 1999) resulting in drastic biodiversity declines and impaired ecosystem functioning (IPBES 2019). Forest area continues to decline at alarming rates in many parts of the world (e.g. Africa and South America), with an estimated 420 million ha of forest lost globally since 1990 (FAO 2020). However, increasing recognition of the paramount importance of forests for biodiversity and human wellbeing has led to a gradual slowing of net forest loss over recent decades, particularly in temperate regions of Europe and Asia. These trends have been largely driven by tree planting schemes leading to a global increase of 123 million ha of planted forest since 1990, although nearly half of this (45%) consists of commercial production forests (FAO 2020). Tree planting is increasingly regarded as a key part of the solution to mitigate climate change and tackle the biodiversity crisis (e.g. Holl & Brancalion 2020), and as such has made its way to the forefront of the environmental agenda. International commitments such as the Bonn Challenge (aiming to restore 350 million ha of forest by 2030) and the UN's upcoming Decade on Ecosystem Restoration 2021-2030, are expected to accelerate and further mobilise action and resources to scale up reforestation efforts globally (IUCN 2019).

In the UK, tree planting has been a priority for more than a century (Harmer et al. 2015), and has contributed to increasing woodland cover from a historic low of 5% at the beginning of the 20th century (down from a post-glacial of ca.70%) to the current figure of 13% (Watts 2006; Forestry Commission 2020a). Tree planting is expected to continue at an accelerated rate, driven partly by the current environmental policy agenda which includes ambitious woodland expansion targets to mitigate climate change and tackle the biodiversity crisis. For instance, the UK Government has pledged to plant 180,000 ha of trees in England over a 25-year period (2018-2042; Defra 2018) and the Scottish Government has a current target of planting 12,000 ha of trees per year, increasing to 15,000 ha from 2024 (Scottish Government 2018). Whilst within the

last 100 years the majority of woodland creation in the UK has been dominated by non-native coniferous plantations (primarily for timber production), there has been a gradual shift towards planting more native woodlands with multiple objectives, recognising the wider environmental, visual and cultural benefits provided by native woodlands (Harmer et al. 2015); for instance, 42% of the 10,860 ha of new woodland planted in Scotland during 2019-20 was classed as native (Forestry Commission 2020a). The majority of these (relatively small) native woodland patches have been planted on former agricultural land (Ferris-Kaan 1995; WEAG 2012). Recently, there has also been increased recognition of the importance of increasing quality as well as quantity of new woodland cover (Woodland Trust 2020) and of enhancing woodland adaptability and resilience (Scottish Government 2019).

Despite decades of tree planting initiatives, we know relatively little about how woodland creation sites (particularly native woodlands) develop over time, how they function and the impacts they have on biodiversity and ecosystem service provision (Fuentes-Montemayor et al. 2015; Harmer et al. 2015; Burton et al. 2018). Whilst successional processes in natural forests and vegetation development in forestry production systems have been well-studied (e.g. Peterken 1996; Kimmins 2004), many of the ecological processes of native woodland creation sites remain poorly understood or quantified (Ferris-Kaan 1995; but see Harmer et al. 2001). These might differ from 'natural' successional processes because of land-use legacies arising from abrupt changes in land-use (e.g. from agriculture to woodland) which can have long-lasting effects on woodland development; for instance, tree growth rates and drought vulnerability are higher in former agricultural areas with highly fertile soils (Alfaro-Sanchez et al. 2019). Legacy effects often depend on previous land-use intensity, for instance with less severe impacts expected by planting on former pasture than on arable land (Holmes & Matlack 2018). Additionally, initial planting conditions such as tree spacing and species composition are also likely to be major determinants of the future trajectory of woodland creation sites, as they will influence tree growth, mortality and

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3 98 survival processes which govern vegetation dynamics (Peterken 1996). Planting methods used
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5 99 for establishing new native woodlands often mimic modern forestry practices which can result in
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7 100 simple homogeneous vegetation structures (e.g. of even-aged species-poor plantations) unlike
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9 101 those of most natural systems, which tend to be more species-diverse and spatially
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11 102 heterogeneous (Ferris-Kaan 1995).
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14 103 The mechanisms driving woodland dynamics change in importance over time. For
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16 104 instance, younger stands (<20 years) tend to be more strongly affected by environmental stress
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18 105 than by other factors (Peterken 1996). Grazing and/or browsing pressure can also be
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20 106 disproportionately important drivers of woodland dynamics during these early stages, when young
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22 107 trees have not yet reached a sufficient height to escape ungulate herbivory damage that might
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24 108 increase tree mortality rates (Rhodes et al. 2017, 2018). Herbivory pressure can continue to be a
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26 109 major determinant of vegetation composition and structure in later development stages when
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28 110 natural regeneration is expected to take place. Interspecific competition usually becomes a more
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30 111 important driver of vegetation dynamics after canopy closure, and natural disturbances such as
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32 112 windthrow become dominant factors in old-growth forests (>200 years; Peterken 1996). The
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34 113 dynamics of woodland creation sites are also likely to be influenced by either a lack of natural
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36 114 disturbance events (e.g. gap formation due to large tree mortality in older and larger sites) or
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38 115 disturbance from forestry practices (e.g. thinning, successive regeneration felling). All these
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40 116 drivers of tree demography dynamics are likely to be reflected in the vegetation structure of a
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42 117 woodland, which in turn will influence woodland biodiversity; for example, variation in tree size
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44 118 (likely to be partly determined by herbivory pressure and management practices) has been
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46 119 identified as one of the main drivers influencing the species richness and abundance of many
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48 120 taxa in woodland creation sites (e.g. Fuentes-Montemayor et al. 2017, 2020; Fuller et al. 2017).
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52 121 Vegetation structural changes are unlikely to be evident in the short term, particularly in
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54 122 temperate woodlands where successional rates and habitat development are slow. This makes it
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imperative, but also challenging, to study woodland ecosystems over sufficiently long temporal scales (from decades to centuries) to detect meaningful structural changes (Harmer et al. 2001). The Woodland Creation & Ecological Networks project (WrEN; www.wren-project.com) is a large-scale 'natural experiment' designed to study the long-term effects (up to 160 years) of woodland creation on biodiversity and ecosystem functioning (Watts et al. 2016). WrEN also provides a unique opportunity to quantify long-term vegetation structural changes in woodland creation sites. Here, we surveyed a chronosequence of 133 temperate woodland patches encompassing secondary (woodland created on former agricultural land between 10–160 years ago; part of the WrEN project) and mature 'ancient' woodlands (continuously wooded for at least 250 years) across England and Scotland. Our overall aim was to assess how the vegetation structure of woodland creation sites develops over time, and how it compares to that of mature ancient woodlands (likely to display structural features more similar to old-growth stages and usually regarded as higher quality habitats for many taxa than woodlands in earlier successional stages; Spencer & Kirby 1992). Specifically, we addressed the following questions:

- 1) Which are the key vegetation attributes driving differences between woodlands of different ages?
- 2) Does the vegetation structure of woodland creation sites resemble that of mature ancient woodlands? And if so, how long does it take for this to happen (as an indication of 'waiting times' from planting trees to delivering woodlands with a more natural, complex structure and potentially higher biodiversity value)?

We expected woodland creation sites within a 10–160 year timespan to display similar development patterns and structures to those described for other woodland systems following major disturbances, i.e. undergoing 'stand initiation', 'stem exclusion' and 'understorey re-initiation' stages (Oliver & Larson 1996). We expected mature ancient woodlands to contain

important components of ‘old-growth’ stages, e.g. a more complex vegetation structure and larger amounts of deadwood (see Fig. 1 for a description of each woodland development stage).

Methods:

Study area and site selection:

Our study sites were in two regions of the United Kingdom (central Scotland and central England) dominated (>70%) by agricultural land and representing fairly typical lowland landscapes in these countries. We used a systematic site selection protocol to minimise variation in topography, climate and soil types across sites (e.g. Land Capability for Agriculture restricted to lowland arable to improved grassland), and the National Forest Inventory (Forestry Commission 2012) to identify 106 broadleaved woodland patches created over the past 160 years on former agricultural land (see Watts et al. [2016] for further details on site selection). We used the Ordnance Survey historic maps collection (EDINA 2013) to determine the approximate date when each woodland was created (i.e. the time period when each woodland patch *appeared* in maps). Woodland creation sites ranged in size (0.5–30 ha) and approximate age (10–160 years old). In addition, we used the Ancient Woodland Inventory (a spatial dataset of sites which have been continuously wooded since at least 1750 in Scotland and 1600 in England; Spencer & Kirby 1992; Forestry Commission 2011) to select mature woodlands with longer ecological continuity. Ancient woodlands were selected with similar characteristics (e.g. patch size, degree of connectivity and amount of surrounding woodland) and located in the same landscapes as the woodland creation sites (Fig. 2). The age gradient of woodland creation sites selected for this study is likely to represent well-recognised developmental stages for temperate woodland habitats (see Fig. 1; Oliver & Larson 1996; Peterken 1996): stand initiation (0-30 years since planting; n=33), stem exclusion (31-80 years since planting; n=29) and understory re-initiation (81-160 years since planting; n=44); ancient woodlands (continuously wooded for >250 years, but likely to be much older; n = 27) are

likely to display structural features more similar to old-growth stages. However, we acknowledge that many ancient woodlands have a long and complex history of management (e.g. coppicing) and may display characteristics of different development stages despite their long continuity of woodland cover.

Vegetation surveys:

We conducted field surveys to characterise the vegetation structure of all woodland sites. Vegetation surveys were conducted using the point-centred quarter method along an edge-to-interior transect, with points established every 15 m along each transect (Ferris-Kaan & Patterson 1992). At each point, a cross of two perpendicular lines (one of them following the direction of the transect) was established to divide the surrounding area into four quarters; within each quarter, we measured the distance from the centre point to the nearest tree (used to subsequently calculate tree density), identified its species and measured its diameter at breast height (DBH; only trees ≥ 7 cm DBH were included). Each point also served as the corner of a 10 x 10 m quadrat used to visually assess understorey cover (% using Domin scale), and a 2 x 2 m quadrat to visually assess woody debris on the ground (index ranged from 1–3; 1 = leaf litter and small twigs ≤ 1 cm in diameter; 2 = larger branches ≤ 10 cm; 3 = coarse woody debris > 10 cm diameter, including fallen trees). Canopy cover (%) was assessed using a sighting tube with an internal crosshair (Ferris-Kaan & Patterson 1992); if the crosshair intersected canopy vegetation, presence of canopy was recorded; this was repeated 10 times at 1-m intervals perpendicular to each of the transect points.

LiDAR surveys:

We used open-access LiDAR data to characterise the three-dimensional structure of a subset of woodland sites (n = 40 sites encompassing all four woodland development stages). LiDAR point cloud data were obtained from the Environment Agency and the Scottish Environmental Protection Agency (see Supplementary Material 1 for further details on data acquisition and processing). Point cloud data were used to create vegetation height distribution plots for individual woodland sites to graphically evaluate the effects of woodland age on vegetation structure. We used the 'VCI' function from the lidR package (Roussel & Auty 2018) on the point cloud data to calculate a vegetation Vertical Complexity Index (VCI, a variant of Foliage Height Diversity [FHD] based on Shannon's index; Ewijk et al. 2011) for each site. We then ran a Pearson correlation test to assess how VCI related to our field-based structural heterogeneity metric (variation in tree DBH). Due to limitations in data availability and the resulting smaller sample size, we did not conduct any further statistical analyses on the LiDAR data; instead, these results are presented for illustrative purposes only (i.e. to complement and support our field data analyses and to exemplify the utility of this method for characterising woodland structure).

Statistical analyses:

We used Linear Discriminant Analysis (LDA) to explore differences in vegetation characteristics among woodland development stages. We selected LDA over other multivariate analysis methods because it is a form of discriminant analysis, i.e. it looks for linear combinations of variables ('vegetation attributes' in this case) to produce discriminant functions that maximise the separation of objects ('woodland sites' in this case) among different classes known *a priori* ('woodland development stages' in this case; Leps & Smilauer 2003). Additionally, LDA produces coefficients to quantify the relative contribution of each of the explanatory variables to the observed separation of objects along each discriminant function; this can provide biological insights into the determinants of the dissimilarity among object classes (e.g. identifying vegetation attributes that

are most influential in driving differences between woodland stage categories). All vegetation attributes described in the *Vegetation surveys* section were included in the LDA; for tree DBH, we included mean (as a metric of tree size) and standard deviation (SD, as a metric of structural heterogeneity) values. In addition, we used linear regressions to quantify differences in individual vegetation variables between woodland development stages (as a categorical factor); significance values were adjusted for multiple comparisons using the Bonferroni correction. Exploratory plots of vegetation attributes and preliminary LDAs indicated that results for the two study regions were broadly similar (Supplementary Material 2); we therefore pooled data across the two study regions for further analyses and we present those results for simplicity. Tree species richness, tree density, understorey cover and tree DBH mean and standard deviation were log₁₀-transformed to improve data distribution prior to analyses. Linear Discriminant Analyses conducted for each study area separately and linear regressions for individual vegetation attributes using 'age' as a continuous (rather than categorical) predictor are presented in the Supplementary Material 2 & 3.

Results:

The vegetation structure of the woodlands included in this study was highly variable. Tree density ranged from 67 to 4063 trees per ha (with an average of 759.7), mean tree DBH from 8.1 to 90.2 cm (average = 29.6), structural heterogeneity (i.e. tree DBH SD) from 1.3 to 43.4 cm (average = 13.7), tree species richness from 1 to 13 (average = 4.8), and canopy cover from 18 to 100% (average = 70.7). Most of these vegetation attributes varied to some degree according to woodland development stage (Figs. 3 & 4); most notably, average tree size and structural heterogeneity (i.e. variation in tree sizes) increased with woodland age, whilst tree density decreased.

The first Linear Discriminant Function (LD1) of the Linear Discriminant Analysis (LDA) showed that there was a 53.6% separation between sites in different woodland development stages, in terms of their vegetation characteristics. The degree of separation explained by LDs 2 and 3 was much lower (11.4% and 1.2% respectively) and is not discussed further. There was a gradual transition in LD1 coefficients from younger to older woodlands, particularly between 'stand initiation', 'stem exclusion' and 'understorey re-initiation' stages, whilst there was a large degree of overlap between sites in 'understorey re-initiation' stage and ancient woodlands (Fig. 3).

The most influential variable (based on its relatively large LD1 coefficient and R^2 value) driving differences between woodland stage categories was variation in tree size (i.e. tree DBH SD), with older woodlands having significantly higher structural heterogeneity (in terms of tree sizes; Fig. 4a). As would be expected, differences in average tree size (bigger in older woodlands) and tree density (lower in older woodlands) also explained a relatively high degree of variability among woodland development stages (i.e. had high R^2 values; Figs. 4b & 4c). There were smaller differences in amount of woody debris, tree species richness, understorey cover % and canopy cover % among woodlands in different development stages (Figs. 4d-4g).

Variation in tree size (our field-based structural heterogeneity metric) was positively correlated with the LiDAR-derived vegetation Vertical Complexity Index (Pearson correlation coefficient = 0.59; $p < 0.001$). In general, the vegetation height distribution of individual woodland sites was in accordance with conceptual expectations based on their developmental stage (Fig. 1); i.e. younger sites in 'stand initiation' were strongly dominated by short vegetation, 'stem exclusion' sites were (less-markedly) dominated by taller trees and ancient woodlands had a more even vegetation height distribution. In accordance with our field data analysis, sites in 'understorey re-initiation' phase appeared very similar to ancient sites, and did not clearly display the two-layer vegetation structure expected as a consequence of natural regeneration (i.e. there appeared to be limited regeneration in the understorey; Fig. 5).

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Discussion:

In this study, we quantified vegetation structural changes occurring in temperate woodland creation sites over a 160-year period after planting on former agricultural land. Our findings show that woodland creation sites display similar development patterns to those described for other woodland systems following major disturbances (i.e. undergoing 'stand initiation', 'stem exclusion' and 'understorey re-initiation' stages; Oliver & Larson 1996). We also compared the vegetation attributes of woodland creation sites to those of mature ancient woodlands with longer ecological continuity.

Development of woodland creation sites and similarities with mature ancient woodlands:

There was a moderate degree of separation between sites in different woodland development stages, driven by vegetation characteristics. As expected, there was a gradual transition in the vegetation attributes of younger to older woodlands, with sites in 'stand initiation' stages progressing towards more advanced stages. Interestingly, there was a large degree of overlap between woodlands in 'understorey re-initiation' stages and ancient woodlands, suggesting that some vegetation attributes of woodlands 80-160 years are fairly similar to those of much older woodlands (>250 years old). This was supported by similarities in individual vegetation attributes between these two late developmental stages. There was also considerable variation within age classes (Supplementary Material 3) suggesting other factors may be promoting (e.g. gap creation due to natural disturbances) or hindering (e.g. herbivore browsing) the development of woodland structures, rather than being driven by age alone. Climatic, topographic and edaphic factors (e.g. soil quality determined by nutrient and moisture regimes; Pyatt et al. 2001) can also play important roles on tree growth rates and consequently on woodland development. As part of our initial site selection process, we attempted to control environmental variation by selecting woodland sites within fairly homogeneous lowland agricultural landscapes (see Methods section and Watts et al.

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3 294 2016 for details). Still, it is possible that some variation persists, but this is unlikely to affect the
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5 295 general patterns observed here. In addition, factors such as degree of land degradation prior to
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7 296 woodland creation (e.g. intensive arable vs. unimproved grassland) and proximity to existing
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9 297 woodland (as a source of propagules) are also likely to strongly influence the structure, function
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11 298 and complexity of woodland creation sites (ongoing work by the authors and others).
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14 299 Structural heterogeneity (i.e. variation in tree size), average tree size and tree density were
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16 300 the attributes that varied the most among woodland developmental stages. Specifically, structural
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18 301 heterogeneity and average tree size increased with woodland age, whilst tree density decreased.
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20 302 However, there was little difference in these attributes between woodlands in ‘understorey re-
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22 303 initiation’ stages and ancient woodlands, suggesting a levelling-off at this point. Whilst young
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24 304 woodlands inevitably have relatively low variation in tree sizes (because not enough time has
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26 305 passed for trees to grow large), the opposite is not necessarily true; i.e. older woodlands which
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28 306 would be expected to have younger smaller naturally regenerating trees to increase size variability
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30 307 could have this inhibited, for example by high browsing pressure or shading. A slight (non-
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32 308 significant) decrease in average tree DBH and increase in tree density from ‘understorey re-
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34 309 initiation’ to ancient woodlands suggests a degree of natural regeneration in the latter that is
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36 310 missing in the younger stage of woodland development. The distribution of vegetation height
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38 311 (LiDAR-derived metric) also indicated differences between most woodland stages, but similarities
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40 312 between ‘understorey re-initiation’ and ancient sites; these similarities appear to result from a lack
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42 313 of regeneration, probably driven by excessive herbivory pressure affecting the understorey layer.
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44 314 However, we did not directly quantify the degree of natural regeneration in our sites and we can
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46 315 only infer it from other vegetation characteristics. Other vegetation attributes which displayed
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48 316 smaller differences among woodland development stages could be more strongly influenced by
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50 317 a combination of herbivory and management factors; for instance, it was surprising that older
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woodlands did not consistently have higher amounts of woody debris or understorey cover than woodlands in earlier successional stages.

Additionally, the significant, positive correlation between our field-based and LiDAR-derived vegetation structural heterogeneity metrics (variation in tree size and Vertical Complexity Index, respectively) corroborates the potential value of using remote sensing data to characterise woodland structure over large spatial scales (e.g. Ewjik et al. 2011).

Importance of woodland management:

Woodland management can greatly alter vegetation structure. For instance, understorey cover (partly driven by natural regeneration) is significantly reduced by the presence of grazing stock in woodland patches (Fuentes-Montemayor et al. 2020) and by deer browsing (e.g. Eichhorn et al. 2017). In Great Britain, 40% of woodland habitat is in unfavourable condition due to herbivore damage (Forestry Commission 2020b); in Scotland, over a third (33%) of native woodlands have such high levels of herbivory (mainly by deer) as to prevent successful regeneration of most tree and shrub species, and 13% have no regeneration at all (Forestry Commission 2014; Forestry Commission 2020b). In addition, only 35% of Great Britain's native woodlands have a 'complex' vertical structure (i.e. are composed of >5 storeys or multiple heights of trees) and 45% have a negligible deadwood component (Forestry Commission 2020b). Whilst we have no direct information on past management in our study sites, there are no signs of recent management interventions (apart from presence of grazing stock in some sites), and we consider intensive past management unlikely given the nature (e.g. small size and agricultural setting) of these woodlands. The sites studied here are fairly small patches (all <30ha, most <5ha) immersed in an agricultural matrix, some of them heavily overgrazed (particularly sites in Scotland). They are characteristic of British woodlands (including ancient semi-natural woodlands of which ca. 70% are <5ha; Woodland Trust 2011). The similarities we found between older woodland creation and ancient woodland sites should not necessarily be interpreted as an indication that they both

represent top-quality habitats. Mature ancient woodlands in the UK have a long history of disturbance and management (e.g. coppicing, felling and removal of deadwood); whilst some disturbance and management regimes positively affect (and are an integral part of) woodland ecosystems, others can have negative impacts on their vegetation structure that persist for centuries (Peterken 1996; Rackham 1980). Larger ancient woodlands managed for conservation purposes are likely to be more structurally complex and of higher biodiversity value than the sites we studied here.

Woodland management practices can also play an important role in improving woodland quality by accelerating woodland development. During ‘stem exclusion’ stages, trees begin to compete with each other for space and light; natural thinning processes take place (i.e. some outcompeted individual trees die, allowing surviving trees to grow larger and resulting in differences in sizes) and structural heterogeneity within the woodland increases. But when all saplings grow at similar rates (i.e. no individuals grow faster to shade neighbours), self-thinning is slow, and a dense stand of slow-growing trees can persist for a long time (Peterken 1996). This is the case of many unmanaged Woodland Grant Scheme sites planted in the early 1990s in Scotland (Fuentes-Montemayor et al. 2015), where a lack of management has led to densely closed canopies with no gaps or light for regeneration to occur. Management activities aimed at promoting natural regeneration on such sites (e.g. through a combination of opening canopy gaps and reducing herbivore pressure) could fast-track woodland development and improve habitat conditions for a range of taxonomic groups (e.g. woodland plants; Harmer et al. 2001; Kerr 1999). Excluding (or minimising) in-site grazing and browsing (e.g. by installing deer-proof fencing) might be particularly important in very young woodlands undergoing ‘stand initiation’, and also during ‘understorey re-initiation’ and ancient stages when canopy conditions would naturally allow seedlings/saplings to develop into new tree cohorts. Tree regeneration is likely to increase structural diversity (in terms of tree age and size distributions) and three-dimensional

heterogeneity. In addition, managing woodlands to promote natural regeneration is likely to enable adaptation through natural selection and enhance woodland resilience to climate change (Whittet et al. 2019).

Biodiversity value of woodland creation sites:

Woodland creation sites provide valuable habitat and resources for a wide range of taxonomic groups including invertebrates, birds, bats and small terrestrial mammals (e.g. Fuentes-Montemayor et al. 2017, 2020; Fuller et al. 2018; Whytock et al. 2018). Vegetation attributes associated with woodland development (e.g. average tree size and variation in tree size) are among the main drivers influencing the species richness and abundance of many taxa, and there is evidence that woodlands become gradually better over time for some species (e.g. bats and small terrestrial mammals; Fuentes-Montemayor et al. 2017, 2020). Our results suggest that there is a 'waiting time' of between 80-160 years from woodland planting to achieving a more natural, complex vegetation structure of potentially higher biodiversity value (although some younger sites had relatively high structural complexity levels, suggesting woodland age is not the only driving factor; Supplementary Material 3). This value can both be enhanced (e.g. by promoting structural heterogeneity; Kerr 1999) or undermined (e.g. by livestock grazing; Lindenmayer et al. 2018) through management activities.

Alternative woodland creation strategies:

Tree planting has been the most common woodland expansion strategy for over a century in countries like the UK (Harmer & Kerr 1995), where overabundant deer populations resulting from a lack of natural predators and control currently put on increased herbivory pressure on woodland vegetation and limit natural regeneration (Gill & Fuller 2007). Planting seedlings/saplings is generally a quicker and more reliable method for establishing woodland than allowing an area to regenerate or to be colonised naturally (Harmer & Kerr 1995; Harmer et al. 2001). But recently in

the UK there have been calls for ‘natural colonisation’ (i.e. allowing trees to colonise new areas naturally) to be incorporated more widely as a woodland expansion strategy (Woodland Trust 2020). Natural colonisation is perceived to lead to more heterogenous and complex woodlands of higher natural value (Harmer & Gill 2000) and also maintain local tree genotypes likely to enable local adaptation to climate change (Harmer et al. 2015; Woodland Trust 2020). The overall similarities between patterns observed here in vegetation development of woodland creation sites and those described for other woodland systems suggest that past land-use legacy effects and initial planting conditions do not preclude the natural development of woodland creation sites over time. Planted sites are also likely to subsequently experience some natural colonisation from nearby woodlands, which will influence the development of these sites through time. These planting sites seem to follow ‘initial floristics’ patterns whereby all tree species establish at approximately the same time after a disturbance (but assert dominance at different times; Egler 1954) and eventually develop into woodlands with some vegetation characteristics similar to those of mature ancient woodlands. However, even if woodland planting sites ultimately resemble semi-natural systems, our results cannot provide information on how they compare to natural colonisation sites (e.g. do the latter reach higher structural complexity more quickly than planting sites?). We suggest that future research should address this knowledge gap. In practice, we advocate that tree planting and natural colonisation should have complementary roles in woodland cover expansion.

Conclusion:

Woodland expansion is widely regarded as a key part of the solution to counteract climate change and tackle the biodiversity crisis. Ambitious environmental policy targets (e.g. to increase woodland cover from 13% to 17% by 2050 in the UK; Committee on Climate Change 2020) often fail to acknowledge the time-lags between habitat creation and its conservation outcomes (Watts

et al. 2020). Our results suggest that it may take 80-160 years for tree planting sites to develop into woodlands with a vegetation structure similar to that of mature, ancient semi-natural woodlands, likely to be of higher biodiversity value than woodlands in earlier successional stages (e.g. Fuentes-Montemayor et al. 2015, 2017, 2020). Woodland management practices to promote natural regeneration and reducing grazing/browsing pressure are likely to accelerate this transition, increase the structural heterogeneity and biodiversity value of woodland creation sites, and enhance woodland adaptability and resilience to climate change. Tree planting is likely to continue to be an integral part of woodland expansion targets in temperate regions; natural colonisation could play a complementary role, but its outcomes are likely to be achieved over longer timescales and be context dependent.

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Supplementary Material:

The following supplementary material is available at *Forestry* online:

Supplementary Material 1: Details on LiDAR data acquisition and processing.

Supplementary Material 2: Results of Linear Discriminant Analyses conducted for each study area (England and Scotland) separately.

Supplementary Material 3: Plots of vegetation attributes of woodlands of different ages (with 'age' as a continuous variable).

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Conflict of interest statement:

None declared.

Data availability:

Data associated with this paper will be deposited in the University of Stirling’s Online Repository for Research Data (DataSTORRE).

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Figure legends:

Fig. 1. Outline of woodland development stages (descriptions adapted from Oliver & Larson 1996 and Peterken 1996). ^a Conceptual changes in the height distribution of vegetation points as woodlands develop over time. Recreated using simulated data based on the study by Ewijk et al. 2011. Colours correspond with height (m) and are for aesthetics only. Strata are shown in 3 m groups for visualisation. ^b >250 years in Scotland and >400 years in England, but likely to be much older; see Methods for details). ^c Whilst ancient woodlands included in this study are likely to display structural features and contain important components of ‘old-growth’ stages, we do not expect them to be an exact representation of this woodland development stage due to past and present anthropogenic impacts.

Fig. 2. Map of Great Britain (A) showing the study areas in Scotland (B, top orange box) and England (C, bottom blue box). Woodland creation sites (circles) are shown according to their development stage: stand initiation (light grey), stem exclusion (dark grey) and understorey re-initiation (black). Ancient woodlands are shown as black triangles.

Fig. 3. Histograms of the first Linear Discriminant function (LD1) coefficients of woodlands in different development stages.

Fig. 4. Boxplots of vegetation attributes of woodlands in different development stages. Different letters represent statistically significant differences between groups ($p<0.05$ with values corrected for multiple comparisons). Y-axes in A-C and E-F have been back-transformed from log10 used in linear models. SI = Stand initiation; SE = Stem exclusion; UR = Understorey re-initiation; AW = Ancient woodland. In E) outliers in stand initiation phase reflect shifts in woodland planting patterns over time (i.e. woodlands created more recently have been planted with a larger number of tree species).

Fig. 5. Height distribution of vegetation points (from LiDAR data) of woodlands in four development stages: stand initiation (a & b), stem exclusion (c & d), understorey re-initiation (e & f) and ancient woodland (g & h). Examples of Scottish (left column) and English sites (right column) are presented. Colours correspond with height (m) and are for aesthetics only. Strata are shown in 3m groups for visualisation.

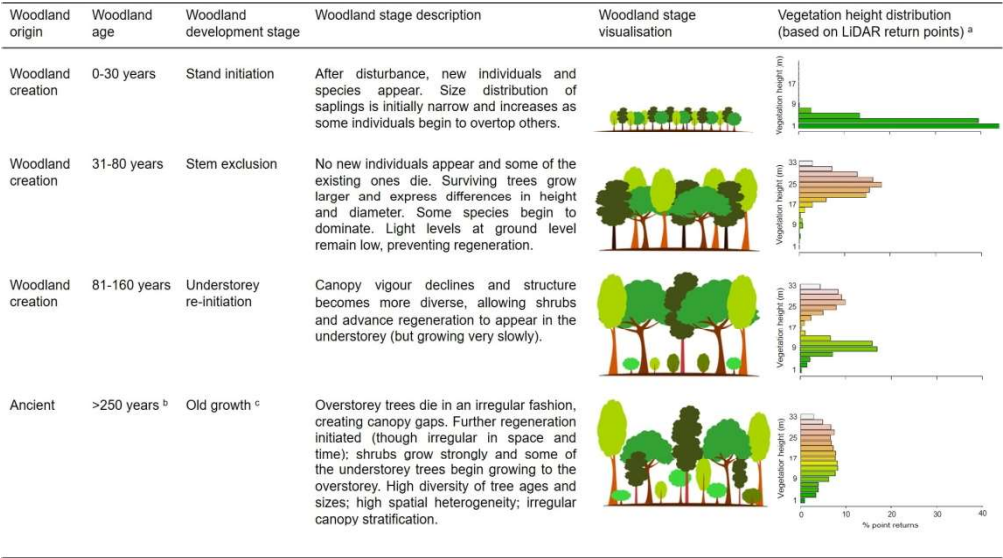


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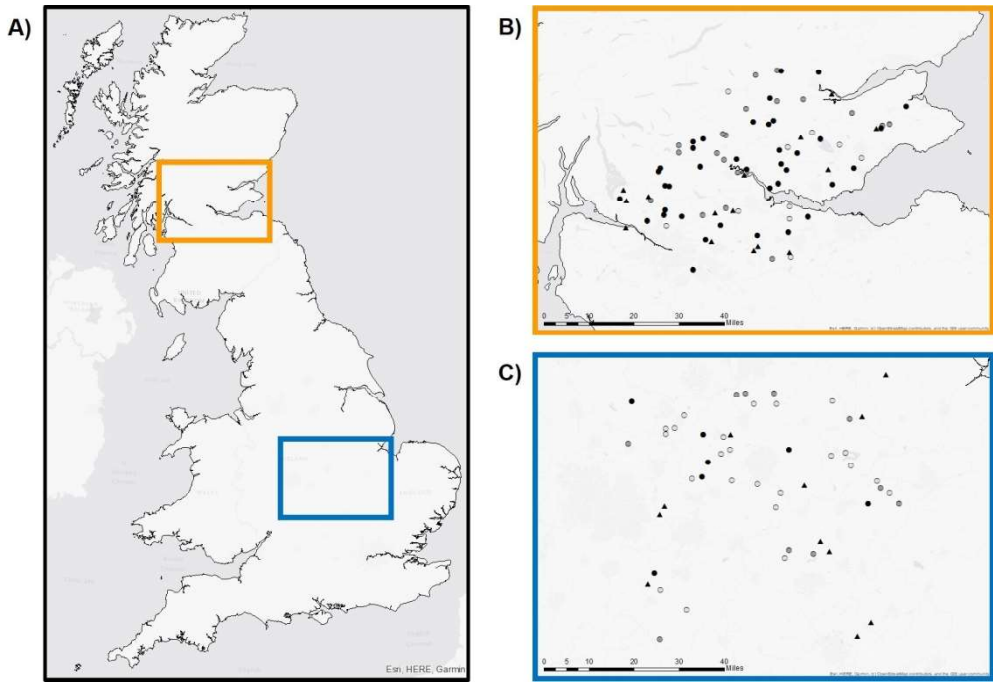


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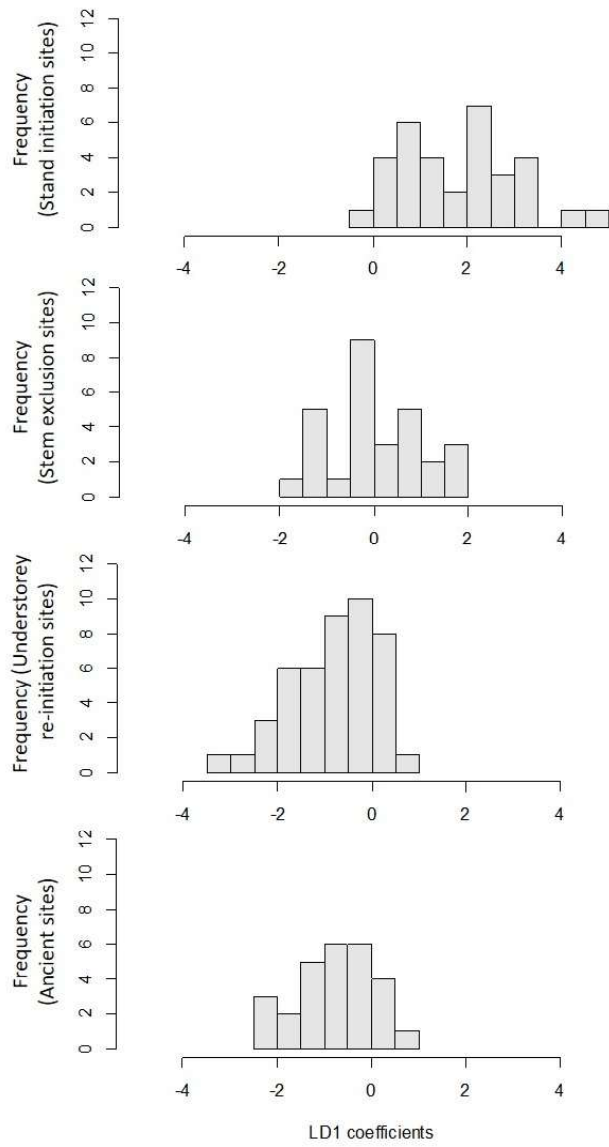


Fig. 3. Histograms of the first Linear Discriminant function (LD1) coefficients of woodlands in different development stages.

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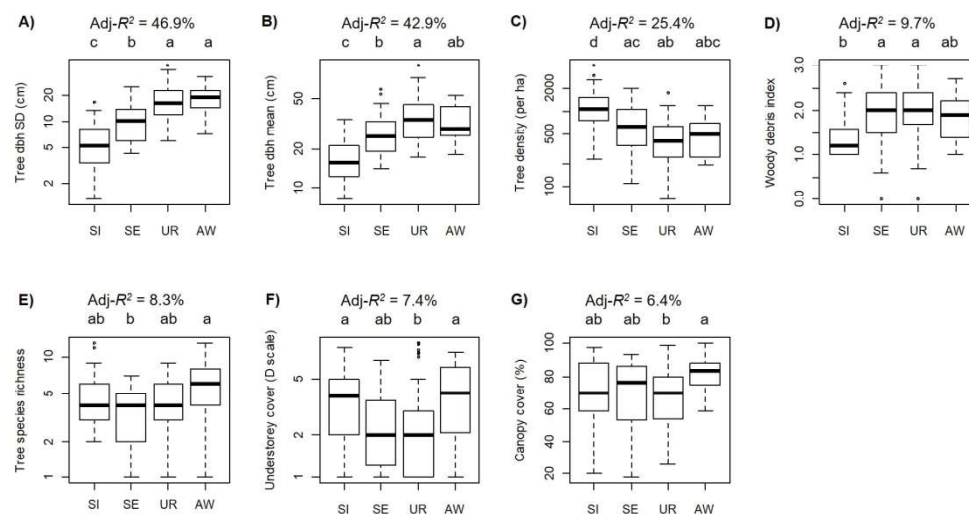


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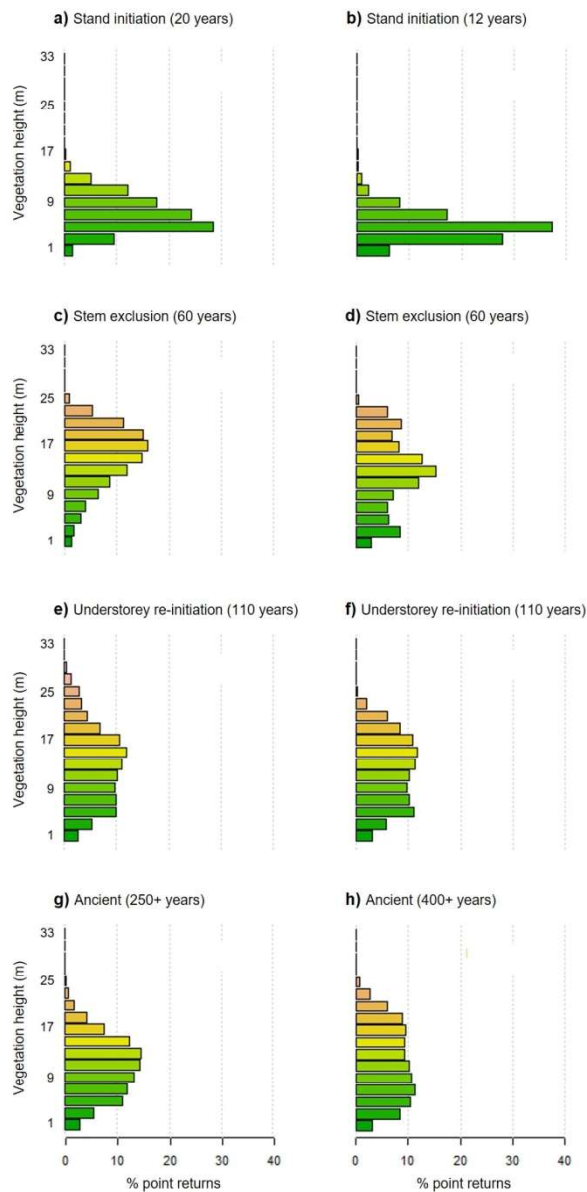


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167x329mm (150 x 150 DPI)